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Author(s)	Jin, Lee
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The Effects of Large-Scale N fertilization on the Interaction between Plants and Herbivorous Insects in a Deciduous Broad-Leaved Forest

JIN LEE

Graduate School of Environmental Science, Hokkaido University, Sapporo, 060-0810, Japan

The Earth's atmosphere is approximately 78 percent nitrogen (N) gas, but most organisms, particularly plants and insects, cannot use N gas directly from the air. Instead, plant must wait for N to be fixed in soil that is pulled from the air and bonded to hydrogen (H) or oxygen (O) to form inorganic compounds (e.g., ammonium (NH₄) and nitrate (NO₃)), that they can use (Vitousek et al. 1997; Galloway et al. 2004). In subsequently trophic level, insects can secure their nourishment from the organic materials synthesized by plants (Vitousek et al. 1997). Therefore, N should serve as one of the major factors to the plants and insects, although atmospheric N is abundant.

During the past century, increased N emission due to human activities including industrial fixation, the combustion of fossil fuels, and the cultivations of legume crops (e.g., soybean, peas, and other crops) is one of the most important threats for planet's environment (Rockström et al. 2009). In fact, the human activities have already doubled the rate of N entering the land-based N cycle, and that rate is continuing to climb (Ayres et al. 1994; Galloway et al. 1995; Mackenzie, 1995; Vitousek et al. 1997; Galloway and Melillo, 1998; Galloway et al. 2004). Thus, the human-driven global change is having serious impacts on terrestrial ecosystems worldwide (Matson et al. 2002).

The nutritional quality of plant is a fundamental determinant of trophic structure, controlling the distribution of biomass between producers (plants) and consumers (insects) (Cebrian et al. 2009). First, ecosystems based on plants of high nutritional quality are characterized by high ratios of herbivorous insects to plant biomass, high herbivore productivity, and rapid rates of nutrient cycling (Olf et al. 2002). Second, high nutritional quality of plants can promote herbivorous insect

diversity, because productive and nutrient rich patches can support the highest herbivore diversity (Olff et al. 2002). Thus, the nutritional quality of plants should stress the importance of N as a factor that limits herbivore performance in terrestrial ecosystem (Hunter, 2016).

In general, N fertilization can exert a variety of bottom-up effects through various mechanisms (Kytö et al. 1996; Throop and Lerdau, 2004; Chen et al. 2010). First, as N is a vital component in the diet of all herbivorous insects, enhanced N concentration in plant tissue by N addition can affect resource utilization by the herbivorous insects or their population density or both (Mattson, 1980; Kytö et al. 1996). Second, N deposition also alter plant-herbivore interactions by affecting patterns of allocation to Carbon (C)-based compound, according to the carbon nutrient balance (CNB) hypothesis that plants allocate proportionately more C to C-based defenses than to growth when resources such as N are scarce; when N abounds, more C is allocated to growth than to C-based defenses, such as condensed tannins and total phenolics (Bryant et al. 1983; Coley et al. 1985). Such compounds often prevent herbivorous insects from enhancing their growth and survival (Kytö et al, 1996). However, these results by the N fertilization experiments have either been small-scale manipulations or focused on saplings or young trees.

Previous studies of insect-plant interactions in artificial N fertilization experiments used saplings or young trees, growing either in a chamber or in a natural system (Hartvigsen et al. 1995; Coleman et al. 1998; Osier and Lindroth, 2004; Koike et al. 2006). However, in mature forests, most biological activity and species diversity is in the canopy (Barker and Pinard, 2001; Nakamura et al. 2014), where plant productivity is higher (Basset et al. 2003; Ishii et al. 2004). Many of the physiological, morphological, and phenological characteristics of woody plants vary depending on the ontogenetic development of the plant (Weiner and Thomas, 2001; Augspurger and Bartlett, 2003; Delagrangé et al. 2004; Nabeshima and Hiura, 2004, 2008; Vitasse, 2013). Consequently, extrapolating from the experimental data obtained from saplings or young trees to predict canopy responses in tall canopy trees will not yield robust results.

The purpose of the thesis is to clarify the effects of large-scale N fertilization on the interaction plants and herbivorous insects in a deciduous broad-leaved forest. To

avoid the problems of the small-scale manipulation and using sapling and young trees, I conducted a large-scale N fertilization experiment (fertilized site, ca. 9 ha), and used mature canopy trees as target species (height >10 m). Particularly, I focus on two different types as target species, an oak species that is one of dominant species in my study site and a typical N-limited species, and an alder species that is one of N_2 -fixing plants. By comparing oak species with alder species regarding as non- N_2 -fixing plant and N_2 -fixing plant, I can clarify the different mechanisms the plant-insect interaction by increased N fertilization with plant traits. To account for the effect of N fertilization on the interaction between plants and their herbivorous insects, I investigated the indirect effect of the N fertilization on herbivorous insects by examining change in the quantity and quality of canopy trees including oak species and alder species. Finally, to consider the interaction plant components and nutrient availability to herbivorous insects, I also investigated tree compositions surrounded target species (oak species) and interactive effect on plant compositions and N fertilization for herbivorous insects' stability.

For measurement of the effects of the relationship between tall canopy trees (oak species (*Quercus crispula*) and alder species (*Alnus hirsuta*)) and its herbivorous insects to the N fertilization, the plant traits and their herbivorous insects in three feeding guilds (chewer, galler, miner) were investigated in each species for 3 years including before the N fertilization. In oak species, in 2013 but not 2014, the N fertilization increased N content and decreased the C/N ratio in leaves. Despite these changes in plant traits in 2013, N fertilization had no effect on herbivorous insects in the same year. However, in 2014, the only diversity index decreased significantly. This suggested that species-specific responses to changes in leaf qualities following the N fertilization, in the form of altered insect fecundity, impact the diversity index of herbivorous insects, albeit with a 1-year lag time. Thus, my large-scale N fertilization experiment showed the time-delayed bottom-up effects of N fertilization on insect community structure. In alder species as a N_2 -fixing plant, the N fertilization decreased LMA of leaf traits, and increased chewing herbivory, although leaf chemical traits (N and condensed tannin) remained unchanged. Moreover, chewing herbivory significantly increased with decreasing LMA. This suggested that the N fertilization affects chewing herbivory through the change in LMA of alder species. Thus, it implies that N_2 -fixing

plants in the same with other plants (e.g., non-N₂-fixing plants) under elevated N deposition will lead to greater feeding activities of chewing herbivory without the change in leaf nutrients (N and C-based defensive metabolites). Finally, we investigated whether tree compositions (tree diversity, tree richness, density, and frequency of conspecific species) and N addition influence the stability of herbivorous insects on a focal plant (oak species). Oak dominance increased the stability of galler's community in only control site, although the dominance did not affect the stability of chewing insects' communities both sites. It suggested that the mechanism driving the diversity-stability relationships might have species-specific response, and N deposition might disturb a positive relationship between stability of galler's community and oak dominance.

Finding with regard to the first research question enabled the researchers to evoke the importance of large-scale experiments and a long-term investigation. As results from described in traits of oak species were different to many previous studies (Chauvet, 1987; Kytö et al. 1996; John and Robert, 2001; Throop and Lerdau, 2004; Jones et al. 2008; Chen et al. 2010) in that N fertilization did not affect herbivorous insects through change in plant traits at the same time. The effect of a lag time in my study could raise the difficulties of understanding the ecosystem complex responses to global changes through small-scale experiments. Therefore, long-term and larger scale experiments are need. Also, findings with regard to the second research, described in the part of alder species, shows a novel explanation and approach about herbivorous insects through change in N₂-fixing plant traits to N addition. The answer that leaf toughness of N₂-fixing plant was decreased by N addition regarding the distinct characteristic and allocation of N₂-fixing plant compared with non-N₂-fixing plants could give novel information. Finally, the finding means, described in part of tree composition and insect stability, the discovery of the interactive effects of resource availabilities by the neighbor tree compositions and N addition on herbivorous insects with feeding specialization. In general, most N fertilization experiments indicated the positive effects on herbivorous insects (Chauvet, 1987; Kytö et al. 1996; John and Robert, 2001; Throop and Lerdau, 2004; Jones et al. 2008; Chen et al. 2010). However, the effects on neighbor composition by addition N could either offset or compensate against the responses of the herbivory. These observations suggest that the traits of each

host plant, functions of associated with the environment, and their interactions have a strongly influence on the herbivorous insects by increased deposition.

The general conclusions can be categorized into the conclusion about the largescale experiment, evaluations of N-limited plant and N₂-fixing plant by the N addition, evaluations of herbivorous insects with feeding guilds and community structure by changing in plant traits of each plant, evaluation of the stability of herbivorous insects' communities in diverse stand in combination with N addition. My study on distinctive plant-insect relationships by a large-scale N fertilization can be interpreted properly and understood in combination with the information presented in the chapters of this thesis.

As described above, these aspects from my study are fundamental to research the effect of global change about N emission on insect-plant interaction in sciences. More applied and experimental fields of my study tended to put more emphasis on the critical and innovative study. Thus, a distinction can be made between academic conceptions and a prediction of global changes on the plant-insect interaction to the future increased N deposition can also be created.